Insects Attacking *Passiflora mollissima* and Other *Passiflora* Species; Field Survey in the Andes

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ABSTRACT

A two and one half month exploration for insects of *Passiflora mollissima* (H.B.K.) Bailey, a problem weed of Hawaiian forests, was made in Peru, Ecuador and Colombia. The "Hawaiian type" of *P. mollissima* was frequently encountered. This form appeared to be within a range of variation expressed in *P. mollissima* in the Andes. Although an assemblage of insects was observed feeding on *P. mollissima* and other Andean *Passiflora* species of the subgenus *Tacsonia*, the fauna was found to be poor in species when compared to the faunas of the tropical lowland *Passiflora*. Few of the *Passiflora* specialist insect groups of the lowlands have moved up to use highland species and there is little indication that *Passiflora* specialist groups have developed in the Andes. The most damaging insect found during the survey was *Pyrausta perelegans* Hampson (Pyralidae). Its larvae, like those of the stamen feeding flies seen on the survey (prob. *Dasiops* spp., Lonchaeidae, and *Zapriothrica salebrosa* Wheeler, Drosophilidae), feed within the flower buds causing them to abort. There was much less flowering and fruiting of *P. mollissima* in the Andes than in Hawaii. Since these flower bud feeders may be responsible for the difference, they could prove useful in limiting the spread of the plant in Hawaii. More exploration is needed to discover organisms capable of reducing the existing stands of *P. mollissima* in Hawaii.

Passiflora mollissima (H.B.K.) Bailey (Passifloraceae) is a perennial woody vine, native to the Andes mountains of South America (Killip 1938). This plant, known as "banana poka" in Hawaii, has become a significant weed in mid and high elevation tropical forests on the islands of Hawaii and Kauai (Wong, unpublished). Banana poka is detrimental because it climbs over the forest canopy and shades the trees with its foliage. In addition, the weight of the plant is thought to physically injure the trees on which it grows. The *Metrosiderous polymorpha* Gaudichaud and *Acacia koa* Gray forests, which it infests, represent the principal native upland forest formations of Hawaii and are found nowhere else. *P. mollissima* is considered to be a major problem in koa forest management. A 1971 survey of the infested areas found that *P. mollissima* comprised from 70 to 100% of the vegetative cover in some places (Wong, unpublished). During a 1978-1981 vegetation survey, banana poka was found to be distributed continuously over 190 km^2, and in more widely scattered populations over an additional 330 km^2 on Hawaii and Kauai islands (Warshauer et al. 1983). It was found growing between 600 and 2000 m elevation and in areas where rainfall does not exceed 5100 mm.

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Control of *P. mollissima* is quite difficult. Chemicals are usually inappropriate, since they also affect native vegetation upon which banana poka grows and for which protection from banana poka is sought. Chemicals have proved useful, however, in combination with mechanical means, in eradicating several small infestations of banana poka discovered on Maui in 1977 (Tanimoto, unpublished). On Hawaii and Kauai, *P. mollissima* has become too widespread for successful mechanical or chemical control (Warshauer et al. 1983).

CLASSIFICATION AND DISTRIBUTION

Some confusion has existed as to which species of *Passiflora* Hawaii's banana poka belongs (La Rosa 1983). Fosberg, of the Smithsonian Institution, Washington, determined (in 1975) specimens of banana poka as being closest to *Tacsonia quitensis* Bentham, which is a synonym of *P. mixta* L. Tillet of the Instituto Botanico, Caracas, Venezuela, determined Hawaii's banana poka as *P. mollissima*. The plant has been listed as *P. mollissima* by St. John (1973) and Neal (1965) in their floras of Hawaii.

I suspect that some of the confusion concerning banana poka's identity arose from the fact that it does not completely fit Killip's (1938) description of *P. mollissima*. Killip's monograph on the American Passifloraceae has been the definitive work on the New World *Passiflora*. The main differences between the Hawaiian plants and Killip's *P. mollissima* is the longer length of the sepals and petals (the limb) relative to the flower tube length, and their somewhat reflexed position with respect to the floral tube. Killip described the tube as ranging from 6.5 to 8 cm in length and the limb from 2.5 to 3.5 cm long, which is approximately a 2.5:1 tube to limb ratio. Plants I measured at Kokee, Kauai, Hawaii had tubes ranging from 6.6 to 7.5 cm long and limbs from 5.1 to 5.5 cm long. Plants growing at Laupahoehoe on the Big Island of Hawaii had tubes 4.3 to 7.5 cm long and limbs 3.6 to 5.3 cm long. The average tube to limb ratio of Hawaiian banana poka was 1.5:1, versus Killip's 2.5:1.

Passiflora mollissima belongs to the subgenus *Tacsonia*, a group of 37 species occurring in the Andes from Venezuela to Bolivia (Killip 1938). *Tacsonia* species are morphologically distinct from other passifloras, bearing long tubular flowers adapted for pollination by hummingbirds. Hawaii's commercial passionfruit (*Passiflora edulis* Sims.) belongs to the subgenus *Granadilla* a relatively distantly related group of lowland species (Killip 1938).

Killip described *P. mollissima's* distribution as follows: western Venezuela and the eastern Cordillera of Colombia to southeastern Peru and western Bolivia, between 2000 and 3200 m altitude, rarely at lower or higher elevations, often in cultivation; also cultivated in Europe, Mexico, and southern California. It is now known to be naturalized in New Zealand, Australia, New Guinea, the Kermadec Islands and East Africa (La Rosa 1983), as well as Hawaii. In the Andes, *P. mollissima* is grown for its fruit, usually in home gardens.

BIOLOGICAL CONTROL

In the mid 1970's, the Hawaii State Division of Forestry evaluated the barnacle scale, *Ceroplastes cerripediformis* Comstock; a thrips, *Selenothrips rubrocinctus* (Giard); and a disease, *Alternaria passiflorae* Simmonds (all three introduced organisms) as potential biological control agents for banana poka, and found them to be ineffective (La Rosa 1983). The American gulf fritillary butterfly, *Agraulis vanillae* L. (Nymphalidae), recently has been introduced and spread in Hawaii (Beardsley, pers. comm.). This butterfly is thought to have low potential as a control agent because of its highly dispersive behavior (Waage et al. 1981).

Waage et al. (1981) did oviposition and larval development tests using eight species of *Heliconius* butterflies (Nymphalidae) on banana poka and commercial passionfruit *(P. edulis)*. *H. melpomene* Bates completed larval development on both banana poka and *P. edulis*, but laid eggs only on banana poka. Since *P. edulis* and *P. mollissima* are separated by more than 300 m of altitude in Hawaii, *P. edulis* would not, presumably, be damaged by *H. melpomene*, unless the butterflies migrated to *P. edulis* after developing on other weedy passifloras such as *P. ligularis* Jusieu and *P. foetida* L. *Heliconius ismenius* Doubleday also laid eggs on *P. mollissima*, but not on *P. edulis*. The *H. ismenius* culture was lost before the completion of the larval development tests. Waage et al. (1981) advocated the use of *Heliconius* species against banana poka because these butterflies are restricted to *Passiflora* species, are habitat specialists, have low dispersive behaviors and high longevity. Most *Heliconius* species occur in hot lowland habitats. It is unknown if there are *Heliconius* species that can survive and prosper at high altitudes where banana poka occurs in Hawaii.

The primary objective of my survey was to discover natural enemies that appeared to have the potential to reduce the standing biomass of banana poka and to limit its reproduction. Insects and diseases with narrow host ranges were sought so that commercial passionfruit *(P. edulis)* growing in Hawaii would not be damaged. Another goal was to find populations of the Hawaiian form of *P. mollissima* to aid in clarifying the pest's identity.

MATERIAL AND METHODS

A two and one half month survey of insects attacking *Passiflora mollissima* and the other closely related *Passiflora* species of the subgenus *Tacsonia* was made in Peru (January 19 - March 14), Ecuador (March 18 - April 10) and Colombia (April 13 - 16). Survey routes (Figures 1 and 2) were selected to allow (1) visits to a large number of literature and herbarium specimen localities for *P. mollissima* and other tacsonias, (2) access by road, (3) time efficiency. I flew between countries and utilized rented 4-wheel drive vehicles to cover the route, except in the Paucartambo valley of Peru, which was surveyed on horseback. The survey was made at a time and sequence to attempt to coincide with periods of high insect activity. Peru, the most seasonal area, was visited in its late summer during the early part of its rainy season, a time of active growth and flowering of highland passifloras.

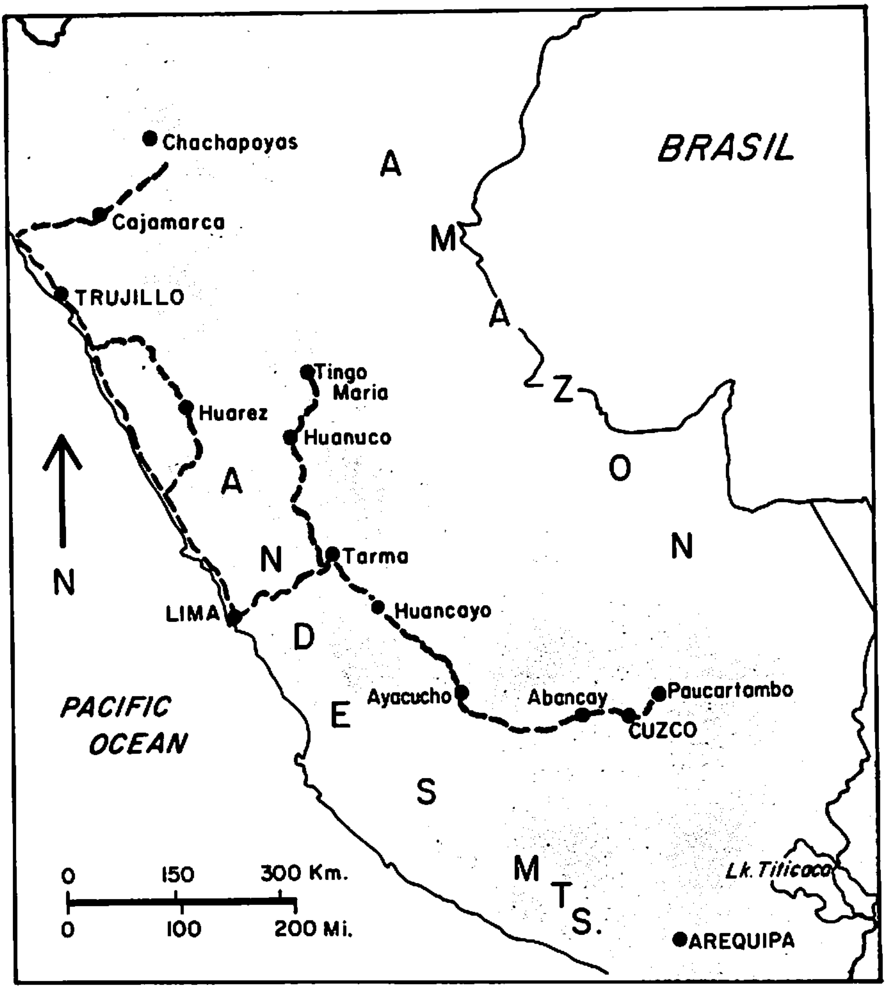

FIGURE 1. Survey route in Peru.

The materials utilized on the survey were standard entomological and botanical field equipment. I carried a dissecting microscope and dixie cups for rearing.

Upon arrival at a site with banana poka or other *Tacsonia* populations, a search for insects and diseases was made by examining the leaves, clipping stems and dissecting flowers, flower buds, and fruit. Since wilting of plants was not observed, and because of the time and labor involved in digging plants, the roots were not normally examined. Since most of the insects were encountered in the immature stages, it was necessary to rear adults for identification. Herbarium specimens and photographs of the insects, their

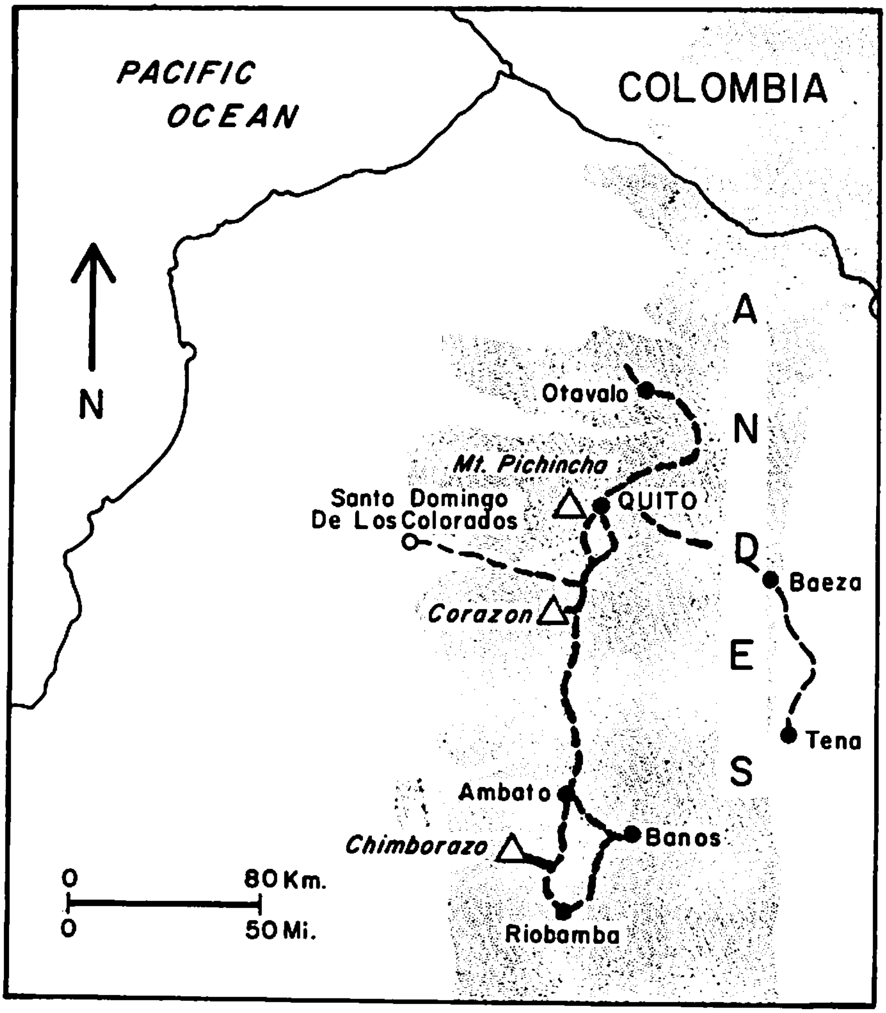

FIGURE 2. Survey route in Ecuador.

damage and the plants were made at most localities.

Identifications of the insect and plant material were obtained from various specialists during and following the survey. Identifications of plant specimens were made or confirmed by L. K. Albert de Escobar of the University of Antioquia in Medellin, Colombia. Identifications of insects were by R. E. White (Chrysomelidae), D. R. Whitehead (Curculionidae), J. M. Kingsolver (Lathrididae), J. P. Kramer (Cicadellidae), R. W. Poole (Arctiidae and Noctuidae) and D. C. Ferguson (Pyralidae); all of the U.S. Department of Agriculture's Systematic Entomology Laboratory in Beltsville, Maryland.

RESULTS AND DISCUSSION

Occurrence of Passifloras. *Passiflora mollissima* was found from ≃ 1,830-3,660 m during the survey. The more usual range was from ≃ 2,750-3,350 m. Since the Andes, especially in Peru, have few level areas, the plants were usually found growing on the slope, with the "paramo" (high altitude herbaceous vegetation) above and rivers far below (Figure 3). *P. mollissima* was almost always found associated with people, frequently planted in gardens and growing in disturbed areas near houses and villages. The vines often grew on trees, usually *Eucalyptus* or *Alnus*, along creeks and drainages. The best indicators of the presence of *P. mollissima* were *Alnus* trees. *P. mollissima* was found at 39 sites in Peru, 11 sites in Ecuador and 2 sites in Colombia. I did not see commercial plantings of *P. mollissima*, as occurs in some parts of Colombia, during the survey.

Passiflora mixta, a closely related subgenus *Tacsonia* species which was also surveyed, occurred in more natural situations than *P. mollissima*, and was not seen in gardens. *P. mixta* was observed between ≃ 2,835-3,445 m, at one site in Peru and at 12 sites in Ecuador. The third most frequently encountered species of *Tacsonia* was *P. pinnatistipula* Cavanilles. It was found in both gardens and in the wild at elevations from ≃ 3,090-3,500 m. This species was observed at 6 Peruvian sites and at one locality in Ecuador.

FIGURE 3. *Passiflora mollissima* habitat in the Peruvian Andes in Ayacucho. *P. mollissima* usually occurred in the 2,750-3,350 m zone, with the treeless paramo at 4,000 m above and desert river valleys at 1,800 m below.

Other *Passiflora* species of the subgenus *Tacsonia* that were examined were: *P. cumbalensis* (Karst) Harms, at 2 sites in Colombia; *P. gracilens* (Gray) Harms at 2 places in Peru; *P. matthewsii* (Masters) Killip, at 4 Peruvian sites; *P. trisecta* (Masters), at 2 places in Peru; and *P. rosea* (Karst) Killip (a hybrid between *P. mollissima* and *P. pinnatistipula*), at 2 sites in Peru.

The Plant Form. During the survey I encountered a range of forms of *P. mollissima* which included plants with broad limbed flowers like banana poka, as well as plants with narrow limbed flowers matching Killip's description (Figure 4). In the Peruvian departments of Ayacucho, Apurimac and Cuzco, only the narrow limbed forms were encountered, except for a white flowered broad limbed form at one site in Cuzco. In the department of Ancash only the broad limbed form was seen and in the department of Cajacamca both forms were found, often within a few kilometers. In Ecuador, both forms were seen without an apparent pattern of occurrence, except that the broad limbed form was more common than it was in Peru. At the end of the survey I visited L. K. Escobar, a specialist on the *Tacsonia* passifloras. She examined the broad and narrow limbed forms I had col-

FIGURE 4. *Passiflora mollissima* flowers (from Cajamarca, Peru) showing the narrow limbed form on the left and the broad limbed form, which is the "Hawaiian form" on the right.

lected on the survey and compared this material with the Hawaiian banana poka, which she had growing in her laboratory. She felt that the plants were within the limits of what could be called *P. mollissima* (Escobar 1980).

The Insects. The most interesting insect found on the survey was the pyralid moth whose larvae were discovered feeding primarily within the flower buds of *Passiflora mollissima* and *P. mixta*. This insect was identified as *Pyrausta perelegans* Hampson by D. C. Ferguson, who noted that the group needs revision. Figure 5 shows a flower bud of *P. mollissima* which has been bored by *P. perelegans* and aborted. In some *P. mollissima* populations, large numbers of these damaged and aborted buds littered the ground beneath vines. Although the larvae were usually found in flower buds, they were occasionally seen in fruits and boring within the tips of shoots. Rojas de Hernandez and Chacon de Ulloa (1982) also have observed *P. perelegans* feeding on *P. mollissima* in Colombia. They observed young larvae boring the terminal shoots and the middle and late instar larvae feeding within the flower buds, young flowers, and occasionally fruit. There appeared to be an increase in the size of flower buds used by larvae as they grew, with the largest larvae usually occupying the larger buds.

Pyrausta perelegans larvae found within flower buds of *P. mollissima* growing at Churcampa, Ocopa, Tarma and Oros, Peru, were reared to the adult

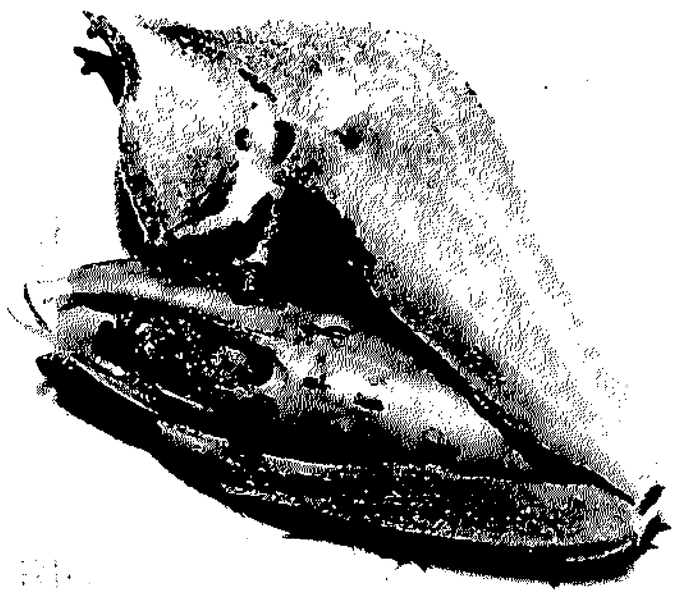

FIGURE 5. An aborted flower bud of *Passiflora mollissima* showing the feeding damage caused by *Pyrausta perelegans*.

stage. The larvae, which were hairless and a shining green or cream color, webbed flower buds together for pupation. Larvae collected at Tarma and Ocopa, formed pupae from the 6th to the 10th of February, and emerged as adults from the 8th to the 10th of March. Rojas de Hernandez and Chacon de Ulloa (1982) reported a 54 day larval period, 16 day prepupal period and a 36 day pupal period. Reared adults of *P. perelegans* usually were cream or light green in color, with small brown flecks. Wild adults were not encountered during the survey. *P. perelegans* was found at 22 sites in Ecuador and Peru. In Peru it was found on *P. mollissima* at 11 sites and on *P. mixta* at 3 sites. In Ecuador it was seen on *P. mollissima* at one site and *P. mixta* at 7 sites. It fed on both broad limbed and narrow limbed forms of *P. mollissima*.

There are a number of significant pest insects belonging to the genus *Pyrausta* including the European cornborer *Pyrausta (Ostrinia) nubilalis* Hübner. However, *P. perelegans* has not been recorded as a pest of any crop and is not known to attack plants other than species of the subgenus *Tacsonia*.

Less *P. mollissima* flower and fruit production was seen during the survey than in Hawaii. Feeding by *P. perelegans* may be one of the reasons for the difference.

Dione juno (Cramer), one of the few heliconiines (Nymphalidae) to occur at high altitude, was one of the most obvious and frequently seen *Passiflora* insects on the survey. The larvae of this butterfly were observed at 30 sites, on *P. mollissima, P. mixta* and *P. gracilens*. Eggs of this species were also seen on *P. mathewsii* and *P. pinnatistipula*. Adults were reared from *P. mollissima, P. gracilens* and *P. edulis*. *Dione juno* has also been recorded from *P. edulis* by Benson et al. (1975). Despite its commonness, the larvae were almost always at low densities and probably had little impact on *P. mollissima*.

Another heliconiine butterfly, a species with black spiny larvae, was observed feeding on *P. mollissima* at six sites. Adults that were reared on *P. mollissima* have been identified as *Dione moneta* Hübner (G. Llama, Lima, Peru) and "possible *D. moneta*" (R. Robbins, USDA Systematic Entomology Laboratory). L. Gilbert (pers. comm.) has indicated that a photograph of the larvae, from which the "*Dione moneta*" adults were reared, depicts *D. juno*, not *D. moneta*. This species was, at times, quite damaging to *P. mollissima*. Large vines in Huaraz, Peru were almost completely defoliated by the gregarious larvae. Escobar reported (pers. comm.) seeing young plants killed by a *Dione* sp. in Colombia. Benson et al. (1976) lists *P. edulis* as a host plant of *Dione moneta*. *D. glycera* Felder and Felder, which resembles *D. moneta* (Gilbert, pers. comm.), has been found on *P. mollissima* in the Andes (Waage et al. 1981).

Leafmines were observed fairly frequently on both *P. mollissima* and *P. mixta* during the survey. They were never very abundant and seemed to cause little damage. Adult moths reared from blotch-mines in leaves of *P. mollissima* were a gracilarid, possibly *Acrocercops* sp. near *pylonias* Meyrick, which was recorded as mining "curuba" (*P. mollissima*) by Posada et al. (1976) in Colombia.

Gregarious arctiid larvae were observed feeding on the leaves of *P. mollissima* at two sites along the Riobamba-Ambato highway of Ecuador on April 3. These colonies contained very small larvae which were not successfully reared to adults. It is not known how much defoliation they normally cause. These may have been *Turuptiana sanguinipectus* Seitz, which was reared from *P. mollissima* in Bogota, Colombia by S. I. de Arivalo of the University of Bogota (pers. comm.), and identified by R. W. Poole.

Larvae of noctuid moth, identified as *Copitarsia* sp. by R. W. Poole, were found feeding within large aborted *P. mollissima* flower buds at Tarma, Peru on January 30th. These were put in dixie cups with *P. mollissima* flowers. On February 6, one larva constructed an earthen cell and formed a pupa, and on March 30 an adult emerged. Chacon de Ulloa and Rojas de Hernandez (1981) reported *Copitarsia consueta* (Walker) attacking *P. mollissima* flowers, in which the larvae feed on the "peduncle that supports the sexual organs causing the flowers to abort." Gallego and Angel (1979) listed *Copitarsia*, possibly *C. consueta*, as eating the leaves of potatoes in Colombia.

A yellow and black striped gregarious caterpillar was observed feeding on *P. mollissima* at Puella, Ecuador on April 1 and near the Santa Rosa road junction of the Riobamba-Ambato Hwy. in Ecuador on April 3. These larvae, which had looping locomotion, were probably geometrids. Like the arctiids discussed above, these were not reared to adults. The potential of this species to damage *P. mollissima* is unknown, but it was not very damaging when I saw it.

Among the Diptera found associated with *P. mollissima* and other passifloras were species of Tephritidae infesting the fruit. Since these fruit feeding tephritids were thought to be polyphagous species with no biological control potential, they were ignored during the survey.

Small Diptera larvae, were observed within the unopened flower buds of *P. mollissima, P. mixta, P. gracilens* and *P. trisecta*. Larvae were often seen in aborted flower buds, as well as in those attached to plants. These larvae may have been the drosophilid *Zapriothrica salebrosa* Wheeler, or a *Dasiops* sp. or spp. (Lonchaeidae), or possibly both. Adult lonchaeid flies frequently were observed within the flowers of *P. mollissima* and other *Passiflora* species. Specimens submitted to the USDA Systematic Entomol. Lab. could not be identified.

Casanas et al. (1981) found in Colombia that 54% of the aborted flower buds of *P. mollissima* had been attacked by *Zapriothrica salebrosa*. Single buds contained from 3-8 larvae. The adults of *Z. salebrosa* fed on the pollen of the flowers. As many as 13 adults were noted in each flower. The females laid eggs on buds which were 60 mm in length. Since *P. mollissima* is the only host plant recorded from the literature, *Z. salebrosa* may be a specialist with biological control potential.

Some of these stamen feeding larvae may have been *Dasiops cucubae* Steyskal, recorded from *P. mollissima* in Colombia (Steyskal 1980). Casanas et al. (1981) found that 80% of the aborted flower buds of *P. edulis* were infested with larvae of a *Dasiops* species. The females deposited eggs on buds ranging from 10-39 mm in length. Although up to 6 larvae were found in a

single bud, there was usually one. Some *Dasiops* species may have biological control potential, if species can be found which use *P. mollissima* and not *P. edulis*.

Almost no weevils were seen on *Passiflora* during the survey. A few adults were found sitting on plants and within flowers. Adults of a *Naupactus* species were seen on *P. mixta* at Papallacta, Ecuador. Several adults of another species (determined as "Genus undetermined, nr. *Amitrus* or *Trichocyphys*" by D. Whitehead) were observed on *P. pinnatistipula* near Pampas, Peru, and on *P. mollissima* at Cajamguilla, Peru. These were held with their "host" passifloras but were not observed to feed.

Similarly, very few chrysomelid beetles were observed on passifloras during the survey. No larvae were encountered and only a few adults were seen. The most numerous species was a bright red *Lactica* species found on the leaves of *P. mollissima* in an area from 13-14 km south of Pampas, Peru. Although many beetles were sitting and mating on the leaves, no feeding or damage was detected. When held for observation, they did some feeding on the flowers and lived for several weeks but produced no eggs. A different species of *Lactica* was collected form *P. mixta* at Papallacta, Ecuador. Other chrysomelids encountered and identified included: an *Epitrix* sp. taken from *P. mollissima* of Churcampa, Peru; the same *Epitrix* species from *P. pinnatistipula* growing near Pampas, Peru and a different species of *Epitrix* from *P. mixta* growing at Papallacta, Ecuador. *Epitrix* species are recorded as pests of many crops in Colombia (Gallego and Angel 1979).

An assemblage of unidentified aphids, whiteflies, spidermites, thrips, psyllids, and a tingid were observed on the survey. None were observed to be numerous or damaging to any of the passifloras on which they were seen. A number of *Empoasca* species (Cicadellidae), 2 of which are apparently undescribed (determined by J. Kramer), were observed on various *Passiflora* spp. One species, with separate red-brown and green color phases, was often seen on *P. mollissima*. This may be *Empoasca dimorpha* Ruppel, recorded from *P. mollissima* in Colombia (Gallego and Angel, 1979). None of these *Empoasca* species did much damage. Most species of *Empoasca*, like other cicadellids, are polyphagous, and many species are crop pests.

Comparison of Highland and Lowland *Passiflora* Faunas. Although many interesting insects, including some with biological control potential, were found during the survey, the *Passiflora* fauna of the Andes was judged to be poor in comparison to faunas associated with lowland *Passiflora* species. Only 3 heliconiine butterflies, 2 at *P. mollissima's* altitudes, were observed on the survey. In the lowlands of the Neotropics, single sites may normally have a dozen heliconiine species (Smiley, pers. comm.) and the most diverse sites can contain up to 20 species (Waage et al. 1981). Similarly, there are complexes of chrysomelids attacking passifloras in the lowlands of Costa Rica (Smiley, pers. comm.). Few chrysomelids were found in the highlands, and the ones which were seen are probably not *Passiflora* specialists. In the lowlands, there are also numerous coreid bugs, including specialists such as *Diator*, which attack various passifloras. No coreids were seen on the

survey. Neither were the *Passiflora* feeding *Josia (Dioptidae)* of the lowlands encountered during the survey.

It appears that the lowland passiflora specialists groups, with the exception of 2 *Dione* spp. (Heliconiine) and some *Dasiops* (Lonchaeidae), have failed to colonize the highlands in which *P. mollissima* and the other *Tacsonia* passifloras grow. Are the *Tacsonia* passifloras chemically or morphologically so different from the passifloras belonging to the lowland subgenera, that they are unacceptable hosts for members of the lowland specialists groups? Probably not. Waage et al. (1981), working with 8 species of lowland *Heliconius* butterflies, found that *P. mollissima* was a more acceptable host for oviposition than *P. edulis* (a lowland species). Six of the 8 butterfly species laid eggs on *P. mollissima*, while 4 of the 8 laid on *P. edulis*. In larval development tests, the plants were equally acceptable with 4 of 7 *Heliconius* species larvae developing on each.

If the tacsonias are acceptable hosts, why aren't they exploited by these species? There are genera of many plant families which, although tropical, have colonized the Andean highlands (*Begonia* (Begoniaceae), *Epidendron* (Orchidaceae) and *Passiflora* for instance). Perhaps the lowland tropical specialist insect groups were unable to "follow" the passifloras to the cool Andes. This may be one of the reasons why it was adaptive for the *Tacsonia* passifloras to colonize and radiate in the highlands.

Why haven't specialist groups of *Tacsonia* feeders evolved in the highlands? Although there has been little work with the Andean *Passiflora* fauna, it does seem that there should already be an indication of such groups if they exist. With the exception of *Lactica, Epitrix, Empoasca, Dasiops* and *Dione*, only single species per genus were found using Andean passifloras. *Lactica, Epitrix* and *Empoasca* are thought to be polyphagous as groups and so probably have little or no subgroup specialization on *Passiflora*. *Dasiops* and *Dione*, which have probably moved up from the lowlands, may have undergone some degree of radiation on the tacsonias.

Perhaps an important reason for the apparent paucity of *Tacsonia* feeding specialists is that, as compared to the lowlands, the highlands have fewer total *Passiflora* species and very few species per unit area (Killip, 1938). In the lowlands, diverse habitats may have as many as 15 *Passiflora* species. There are not that many highland *Passiflora* species which are sympatric. A single habitat may have (at most) a couple of species. Many tacsonias are limited to specific altitudinal zones and many are endemic to a single area. These differences may be important in the evolution of specialized groups of *Passiflora* feeders. In the lowlands, there are many *Passiflora* niches in each habitat. When a new or trophically modified form of a specific *Passiflora* feeder appears, there are many plants, closely related to its usual host, already present in its habitat to absorb and "select" the new form. Radiating *Passiflora* insects have many more evolutionary "options" (i.e. new *Passiflora* host) in the lowlands than in the highlands.

The members of the specialized groups probably compete within and outside of their groups, resulting in a finer partitioning of the *Passiflora* resource. This can select for greater plant species and habitat specificity, as

well as a greater division of the plant body utilized. This may result in even more specialized guilds of insects, such as the stamen feeding *Dasiops.*

The presence of large number of *Passiflora* species within single lowland environments may allow *Passiflora* insects to survive and perhaps continue to flourish, even if their preferred hosts become unavailable. In the highlands, when a *Passiflora* becomes unavailable to the insects that normally use it, there may be no other suitable *Passiflora*, causing the insects either to disperse or perish.

These differences may explain why the lowlands appear to have more species of insects using *Passiflora* species, as well as more diversity in the types of feeders, probably greater numerical stability, and less dispersive types of behavior in the insects using *Passiflora* (one of the differences between the highland *Dione* and lowland *Heliconius*).

An important effect of these differences could mean that lowland passifloras are more greatly stressed by insects than the highland species. An indicator of this stress difference may be the amount of flowering, since highly stressed perennial plants usually produce fewer flowers. Smiley (pers. comm.) reports that in the Costa Rican lowlands, many *Passiflora* species flower very little or not at all. In my own limited experience in the Peruvian Amazon, I saw a number of lowland *Passiflora* species which bore no flowers. In contrast, flowerless tacsonias were rarely encountered in the highlands.

CONCLUSIONS

The relative paucity of *Passiflora* insects in the Andes does not mean that the potential for biological control of banana poka is low. The *P. mollissima* populations examined in the Andes were attacked by a number of promising species. The plants were less robust and bore fewer flowers than the *P. mollissima* of Hawaii. These differences, particularly less flowering, may be due to the attack of insects. *Pyrausta perelegans* could (if specific enough to use) limit the degree of shoot growth and, more importantly, reduce flowering and fruiting, as might the *Dasiops* and *Zapriothrica* stamen feeders. A significant reduction in fruit production of banana poka in Hawaii could slow the plant's spread. Additional exploration is needed to discover natural enemies that could damage whole plants and thereby reduce the existing populations of banana poka in Hawaii.

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